

Dominance by an obligate annual affects the morphological characteristics and biomass production of a planted wetland macrophyte community

Alicia R. Korol and Changwoo Ahn*

Department of Environmental Science and Policy, 4400 University Drive, MS5F2, George Mason University, Fairfax, VA 22030, USA

*Correspondence address. 4400 University Drive, MS5F2, George Mason University, Fairfax, VA 22030, USA.

Tel: +1-703-993-3978; Fax: +1-703-993-1066; E-mail: cahn@gmu.edu

Abstract

Aims

Biodiversity–ecosystem function experiments can test for causal relationships between planting diversity and community productivity. Planting diversity is routinely introduced as a design element in created wetlands, yet substantive support for the finding that early diversity positively affects ecosystem functioning is lacking for wetlands. We conducted a 2-year diversity–productivity experiment using freshwater wetland mesocosms to investigate community biomass production as affected by planted macrophyte functional richness.

Methods

A richness gradient of macrophytes in four emergent wetland plant functional groups was established in freshwater mesocosms for two consecutive years. Species-specific aboveground morphological traits of plant size were measured at peak growth in both years; rooting depth was measured for each species in the second year. Aboveground biomass (AGB) and belowground biomass (BGB) were harvested after peak growth in the second year; first year AGB was estimated from morphological traits in constructed regression equations. Net richness effects (i.e. both complementarity effects and selection effects) were calculated using an additive partitioning method.

Important Findings

Species richness had a positive effect on community AGB relative to monocultures in the first year. In the second year, mean AGB was significantly reduced by competition in the most species-rich mixtures

and all mixtures underyielded relative to the average monoculture. Competition for soil resources was weaker belowground, whereby root distribution at depths >20 cm was reduced at the highest richness levels but overall BGB production was not affected. Changes in species biomass were strongly reflected by variation in species morphological traits, and species above and belowground performances were highly correlated. The obligate annual (*Eleocharis obtusa*), a dominant competitor, significantly contributed to the depression of perennial species' growth in the second growing season. To foster primary productivity with macrophyte richness in early successional communities of created wetlands where ruderal strategies are favored and competition may be stronger than species complementarity, unsystematic planting designs such as clustering the same or similar species could provide protection for some individuals. Additionally, engineering design elements fostering spatial or temporal environmental variability (e.g. microtopography) in newly created wetlands helps diversify the responses of wetland macrophyte species to their environment and could allow for greater complementarity in biomass production.

Keywords: complementarity effect, created wetland, macrophyte richness, morphological trait, plant biomass, diversity–productivity relationship

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INTRODUCTION

Accumulating evidence suggests that the trends in local and global biodiversity loss will negatively impact important

ecosystem processes within the carbon cycle (Handa *et al.* 2014; Hooper *et al.* 2012; Isbell *et al.* 2011; Reich *et al.* 2012). Between 2004 and 2009, the USA lost 62 300 acres of wetland habitat and its associated biodiversity in the conterminous

USA from wetland conversion (Dahl 2011). Where wetland habitat was or will be re-established from compensatory creation or restoration, reductions in naturally occurring diversity levels and primary production may still be sustained for decades to come (Ballantine and Schneider 2009; Dee and Ahn 2012; Stefanik and Mitsch 2012). Introducing plant structural and functional diversity early in these new wetlands ecosystems, a common strategy for restoration practitioners, may accelerate the re-initiation of carbon-related ecosystem functions, such as primary productivity (Clewett and Aronson 2008). Using manipulated biodiversity–ecosystem function experiments, we can test for causal relationships between planting diversity and primary productivity and gain insight into the facilitative and competitive interactions that drive community dynamics through species-level investigations (Naeem 2006).

Within a biodiversity–ecosystem function paradigm, positive plant diversity–productivity relationships are a product of one or more of the following mechanisms of species coexistence: niche partitioning, facilitation and the presence of species with unique traits and relative abundances (Hooper *et al.* 2005; Loreau *et al.* 2012; Tilman *et al.* 2001). Species groups that can more fully extract available resources by exploiting a greater number of niches than groups with fewer species can lead more diverse communities to higher productivity (Cardinale 2011; Gross 2007). Alternatively, interspecific processes by which species directly or indirectly facilitate the growth of neighboring species can promote greater community productivity (Bertness and Hacker 1994; de Kroon *et al.* 2012; Le Bagousse-Pinguet *et al.* 2012; Vanelander *et al.* 2009). Where species demonstrate concomitant high productivity, competitiveness and dominance, positive diversity–productivity relationships are supported by individual functional traits (Fox 2005; Wardle 1999). The additive partitioning method by Loreau and Hector (2001) mathematically operationalizes these mechanisms into emergent effects at the community level—complementarity effects, encapsulating predominant niche partitioning and facilitative processes and selection effects, reflecting species unique influences—and has permitted greater investigation and understanding of plant diversity dynamics.

Cardinale *et al.* (2007) synthesized previous research in plant communities and found that mixtures were on average 1.7 times more productive than the average monoculture due to selection effects and to equal or greater contributions of complementarity effects. Many researchers have been interested in the relative balance between these two components, particularly with an interest in finding evidence for long-term structuring forces. Theory and empirical evidence suggest that the importance of opportunistic, single-species processes should give way to more stabilizing forces as plant communities mature and reach carrying capacity (Fargione *et al.* 2007; Pacala and Tilman 2002; Turnbull *et al.* 2013; Weis *et al.* 2007). Yet, the suite of factors that affect group complementarity, such as the right combination of species, the

magnitude of species or functional richness and the response variable of interest, frustrate our abilities to predict the direction of strengthening multispecies interactions (e.g. complementarity, interference) (Balvanera *et al.* 2006; Doherty *et al.* 2011; Hooper and Vitousek 1997). In a study using freshwater-planted mesocosms, Bouchard *et al.* (2007) found that species functional group richness positively affected community belowground biomass (BGB) while not influencing net aboveground biomass (AGB). In another wetlands mesocosm study, Schultz *et al.* (2012) found greater biomass at the highest functional group richness level though this effect was not present for AGB in mixtures at lower richness levels. Other studies in wetlands have also demonstrated the existence of positive diversity–productivity relationships but inconsistent incremental changes from one richness level to the next (Callaway *et al.* 2003; Sullivan *et al.* 2007). Due in part to a paucity of research conducted in wetlands, further investigation of the nature of macrophyte diversity effects on primary productivity is needed.

Species morphological and functional traits related to growth, competition and life history strategy may help explain and formulate hypotheses on the general drivers of community-level productivity. The utility of functional trait–productivity relationships, however, is dependent on the consistency of species interactions across abiotic and biotic gradients. Both above- and belowground strategies to acquire resources determine a plant's ability to coexist with neighbors. For instance, spatial and phenological differences in shoot or root morphology may support complementarity in realized niche space through the evasion of light or nutrient competition (Dimitrakopoulos and Schmid 2004; Fargione and Tilman 2005; Hutchings and de Kroon 1994; Wacker *et al.* 2009). The importance of either mode of competition depends on how plant size and form affects shading and on levels of belowground resources, but whether or not an interaction exists between plant above- and belowground competitive strategies contributes to the uncertainty in species functional performances and their effect on community productivity (Bessler *et al.* 2009; Kiaer *et al.* 2013). Similarly, morphological plasticity as observed between mixtures and monocultures may help a species preemptively acquire limiting resources (Berendse 1982; Barnes *et al.* 1990; Schmid and Bazazz 1994). A positive change in morphological traits in the presence of neighbors, such as height, canopy area and leaf shape may indicate a competitive effect of a species and explain its resulting dominance in mixture (Gaudet and Keddy 1988); however, whether these competitive behaviors maintain functional yield levels may be species-specific (Thein *et al.* 2008). Tracking the commonality of species morphological changes and biomass allocation to community productivity can improve our understanding of selection and complementarity effects observed at the community level.

We conducted a 2-year diversity–productivity experiment with freshwater wetland mesocosms using a replacement series design to investigate changes in plant community

performance across a macrophyte richness gradient. Our primary goal was to study the link between the functional performances of species and the biomass production of the community across two major axes of variation in diversity–productivity experiments: duration of study and medium of plant interaction. We first investigated whether species morphological characteristics and biomass production varied by growing season and differed above- and belowground. We chose a root core sampling method that would specifically allow us to determine the consistency in species above- and belowground functional responses. We then linked the species performance to changes at the community-level using an additive partitioning method. We finally asked whether a suite of commonly measured aboveground morphological traits (universal and specific) could be useful predictors of both species and community biomass production across a gradient of species richness. Specifically for created wetlands characterized by lower functionality in carbon-related properties (Hossler and Bouchard 2010), this study will improve our understanding of macrophyte community productivity and its relevance to carbon processing. The practical application of our results will also inform restoration strategies intended to promote productivity in planted macrophyte communities in newly created wetlands.

MATERIALS AND METHODS

Experimental design

The experiment was conducted using a set of 34 research mesocosms, 568L Rubbermaid tubs with a 1.11 m² surface area each, that sit aboveground in the Ahn Wetland Mesocosm Compound at George Mason University, Fairfax campus. Mesocosms were bottom filled to 20 cm with layers of first river pea gravel and then sand, and topped with 30 cm of locally produced screened, silty-loam topsoil (1.5% total carbon and 0.11% total nitrogen composition) from the Stone Center in Manassas, VA. Retention of or amendments with topsoil are common practices in wetland creation in the Virginia Piedmont physiographic region and are implemented to augment soil nutrient pools which are often limiting in these new ecosystems (Bruland and Richardson 2004; Stauffer and Brooks 1997). Water levels were determined by precipitation events and were periodically supplemented with dechlorinated tapwater in the hottest weeks of summer to maintain a minimum of 5 cm standing water.

In early May 2012, mesocosms were planted with four plugs in a linear array using a combination of four functionally distinct herbaceous wetland plant species: *Eleocharis obtusa* (Willd.) Shult. (obligate annual), *Mimulus ringens* L. (facultative annual), *Juncus effusus* L. (interstitial reed) and *Carex vulpinoidea* Michx. (interstitial tussock) (Boutin and Keddy 1993). Species functional trait differences increase the likelihood that a species combination will use resources more efficiently and maximize community performance (Diaz and Cabido 2001). When selecting planting diversity, classifications of functional

attributes can be useful tools to simplify the complexity of plant species' ecological roles on multiple scales. The planting density, appropriate for ~1 m² mesocosms, was chosen to encourage maximum growth of species and be realistic of planting schemes used for restoration (Ahn and Mitsch 2002). All plugs were of similar size at the start of the experiment. Each of the four species was assigned two monocultures, for eight mesocosms at the lowest richness level (one functional group represented: FG 1); FG 2 had all unique two-species combinations with six mesocosms; FG 3 had all unique three-species combinations with 12 mesocosms; and FG 4, the highest richness level, had eight mesocosms with all species represented. Although the treatment effect of species richness was not independent of species composition, the functional performance and contribution of each species to mixture biomass production could be tracked with adequate replication. The constructed species functional richness gradient was preserved by weeding.

Freshwater herbaceous wetland plant species were selected with two criteria in mind, that they be commonly found in or commonly sowed in created mitigation wetlands in the Virginia Piedmont, and that they be classifiable within either a ruderal or interstitial functional group. Species displaying characteristics of the matrix functional group were excluded from the experiment due to their aggressive growth (Bouchard *et al.* 2007). Both ruderal species flowered in the first growing season and completely died back aboveground in the nongrowing season demonstrating annual behavior. Reeds and tussocks are classified as interstitial perennials, a group distinguished by low percent flowering in the first year and a clumped growth form with some lateral spread (Boutin and Keddy 1993). Both *J. effusus* and *C. vulpinoidea* first flowered at the start of the second growing season. *Carex vulpinoidea*, fox sedge, was not part of the original 43 species classification but displays the morphological and phenological traits characteristic of tussocks.

Morphological measurements and biomass

Morphological traits of plant size were selected for each species based on their unique growth form and were measured once each growing season in late July or early August (Table 1). For instance, 'basal circumference' was measured for *E. obtusa* in the first year because the planted plugs 'tillered' outward in discrete clumps, the size of which reflected increased somatic growth; in the second year, all *E. obtusa* growth was either second or third generation population growth and discrete clumps were gone. Cover was measured as the presence or absence within linked 7 cm length square quadrats. Peak biomass was used as a proxy of plant productivity and was harvested in early September 2013 in the second growing season. All AGB was cut at the soil surface and weighed by species in the compound (± 10 g). Subsamples (~100–300 g) of the species biomass were dried at $\leq 60^\circ\text{C}$ to a constant weight, and dry/wet ratios were used to derive the total dry mass (DM) of species biomass.

Table 1: statistical results for tests of differences in morphological traits and aboveground biomass for the sedge, obligate annual, reed, facultative annual and the community between richness levels (FGs 1–4)

Species traits	First year				Second year			
	Test	Statistic	df	P	Test	Statistic	df	P
<i>Carex vulpinoidea</i> (S)								
Canopy diameter (cm)	<i>F</i>	2.51	3,30	0.078	<i>F</i>	45.1	3,30	<0.001**
Canopy height (cm)	<i>F</i>	1.62	3,30	0.206	<i>F</i>	10.4	3,30	<0.001**
Basal circumference (cm)	<i>F</i>	2.07	3,30	0.126	<i>F</i>	6.16	3,30	0.002**
Cover (cm ²)	<i>F</i>	.937	3,30	0.435	<i>F</i>	5.34	3,30	0.005**
Aboveground biomass (g)	<i>F</i>	5.90	3,30	0.324	<i>F</i>	11.1	3,30	<0.001**
<i>Eleocharis obtusa</i> (OA)								
Canopy height (cm)	<i>F_w</i>	.598	3,18	0.625	<i>F_w</i>	1.22	3,18	0.331
Basal circumference (cm)	<i>F</i>	7.23	3,30	0.001**	—	—	—	—
Cover (cm ²) ^a	<i>F_w</i>	1041	3,12	<0.001**	<i>F_w</i>	36.3	3,7	<0.001**
Aboveground biomass (g)	<i>F_w</i>	961	3,14	<0.001**	<i>F_w</i>	40.7	3,12	<0.001**
<i>Juncus effusus</i> (R)								
Stem length (cm) ^b	<i>F</i>	1.02	3,30	0.397	<i>F</i>	1.31	3,30	0.291
Basal circumference (cm)	—	—	—	—	<i>F</i>	0.972	3,30	0.419
Stem count	<i>F</i>	2.81	3,30	0.056	—	—	—	—
Cover (cm ²)	<i>F_w</i>	1.60	3,12	0.240	<i>F</i>	12.2	3,30	<0.001**
Aboveground biomass (g)	<i>F</i>	0.579	3,30	0.633	<i>F_w</i>	9.72	3,13	<0.001**
<i>Mimulus ringens</i> (FA)								
Stem length (cm)	<i>F</i>	5.93	3,30	0.003**	<i>F</i>	12.1	3,30	<0.001**
Stem count	<i>F</i>	2.10	3,30	0.121	<i>F</i>	4.40	3,30	0.011*
Cover (cm ²)	<i>F_w</i>	20.6	3,12	<0.001**	<i>F</i>	67.9	3,30	<0.001**
Aboveground biomass (g)	<i>F</i>	5.90	3,30	0.003**	<i>F_w</i>	108	3,13	<0.001**
Mesocosms (C)								
Aboveground Biomass (g/m ²)	<i>F_w</i>	0.738	3,13	0.548	<i>F</i>	3.68	3,30	0.023*

^aSquare-root transformed. ^bEstimated from an average of 20 randomly selected stems.

P* values significant at $\alpha = 0.05$. *P* values significant at $\alpha = 0.01$.

Belowground sampling immediately followed aboveground harvesting. Using 7.62 cm diameter soil core samplers (steel duct pipes), one sample from the original location of each planted plug (= 4 cores per mesocosm) was taken to a depth of 30 cm and partitioned at 10 cm intervals. The cores fell within or encompassed the basal area of each planted individual. Root sections were washed and sieved to 2 mm and dried at $\leq 60^\circ\text{C}$ to a constant weight (Bledsoe *et al.* 1999). Intact, recently dead tissue that clearly resembled the live tissue in shape and size (and not amorphous organic debris) was retained. Each core was predominately comprised of one species so we assigned the BGB in each core to the planted individual sampled. Our sampling scheme provides species-specific information but may overstate the BGB estimates for the reed and sedge whose root densities were likely highest directly beneath their culm clusters. Community AGB and BGB, from species data aggregated to the mesocosm level, were scaled to 1 m², with BGB values weighted by species relative aboveground percent cover.

The productivity and morphological traits of both species and communities were of interest. At a species level, the focus of analysis was the planted individual of the species,

defined here as the growth attributable to or partitioned between the four originally planted plugs per mesocosm. An individual assessment permitted examinations of trends in species-level performance across richness levels accounting for differences in species relative abundances, as well as provided a cross-walk to the partitioning of species richness effects on the basis of species relative yields in biomass production (see 'Partitioning effects of macrophyte richness' section). To visually compare the magnitude of species relative yields in mixtures using a common metric, we used the related calculation for proportional deviation which standardizes the change in yield by the expected value:

$$D_i = (O_i - E_i) / E_i,$$

where D_i is the proportional deviation in a species biomass production on the basis of the original planting density of individuals, E_i is the expected biomass production of a species on the basis of monoculture production and the number of individuals of that species planted and O_i is the observed biomass production in mixture.

We also investigated the predictive power of species morphological traits on species and community AGB with

standard multiple linear regression equations. All measured traits were included in multiple regression equations of species AGB in the second year. First-year (Yr1) peak AGB of each species was estimated from these regression equations constructed from second year (Yr2) data (See Morphological traits predict community biomass production). We pooled species data independently of richness level to estimate Yr1 AGB. The community AGB prediction equations were constructed using the most diverse mesocosms (FG 4), which had a sufficient number of replicates, using one trait per species. Traits were first screened for a significant and strong correlation (Pearson $r > 0.7$) with their respective species' AGB in FG 4 mesocosms.

Partitioning effects of macrophyte richness

Mixtures were assessed for differences in species interactions and resulting community performance using an additive partitioning method (Loreau and Hector 2001) where net richness effects on mixture productivities are split into complementarity and selection effects (terms 1 and 2 on the right-hand side, respectively):

$$\Delta Y = N \overline{\Delta RYM} + N \text{cov}(\Delta RY, M),$$

where ΔY = net effect of richness on biomass yield (g DM/m²); N = number of species; ΔRY = deviation from expected relative yield of species i ; M_i = monoculture biomass of species i ; $\text{Cov}(a,b)$ = covariance. The net richness effect (NE) equals the difference between the observed and expected biomass for a mixture. Any mixture that exceeds (or falls below) the average monoculture production nontransgressively overyields (or underyields). Transgressive overyielding, in the case where mixture biomass exceeds the highest producing monoculture, is distinguished as a stronger measure of community performance (Hector *et al.* 2002a). Positive selection effects occur when species with above-average biomass in monoculture overyield (i.e. positive proportional deviations in biomass production); negative selection effects occur in the reverse scenario where species with below-average biomass in monoculture overyield. A positive complementarity effect indicates that, on average, resource partitioning or facilitation is significant enough to cause species overyielding and elevated community performance; a negative complementarity effect indicates that, on average, species were inhibited by their neighbors and the performance of the community suffered.

Data analysis

Standard multiple regression equations using species morphological trait predictors were constructed and were used to estimate Yr1 species AGB and Yr2 community AGB. Morphological trait data were first screened for multivariate outliers, and then for multivariate normality, linearity and heteroscedasticity. Morphological traits, species AGB and BGB and community AGB and BGB were assessed

for mean differences between richness levels (FGs 1–4). Partitioned richness effects (CE, SE, NE) of species above- and belowground yields were assessed for mean differences across mixture richness (FGs 2–4). One-way analysis of variance (ANOVA) was used to determine significance of mean differences. Data were screened for normality with the Shapiro–Wilks test and homogeneity of variance with the Levene test, and with consideration of the central limit theorem and sample size. When data exhibited unequal variance, Welch (F_w) test of equality of means was used. We tested *post hoc* pair-wise differences with the Bonferroni and Games–Howell *post hoc* tests, for equal and unequal variance, respectively. Transformations were used to improve normality. All statistical tests were run in SPSS statistics software v.18 (SPSS 2009) and assessed at an $\alpha = 0.05$.

RESULTS

Species morphological traits and biomass

Proportional to their original planting density, two of the four species performed better in mixture than in monoculture in the first year (Table 1; Fig. 1a). *E. obtusa* increased AGB in all mixtures, cover in FG 4, and its 'basal circumference' in FG 2 and FG 4 as a result of tillering compared to in monoculture. At each richness level, *E. obtusa* also produced the most biomass of any species. *M. ringens* achieved greater AGB in FG 2 and FG 3 than in monocultures, as well as greater average stem length in FG 3 and FG 4 and greater cover for FG 2. *J. effusus* exhibited a trend-wise increase in the number of stems in FG 2 mixtures ($P = 0.056$), but otherwise exhibited no substantial changes in morphological traits or AGB. *C. vulpinoidea* became slightly leaner across richness levels as it decreased in canopy diameter and AGB but these relationships were not statistically significant.

In the second year, fitness levels of all species except *E. obtusa* were adversely affected by increasing community richness (Tables 1 and 2; Fig. 1b and c). The AGB of *M. ringens* decreased in all mixtures compared to in monoculture, in addition to mean declines in FG 4 of stem height, stem count and cover. The BGB of *M. ringens* was also reduced in FG 4 compared to in monoculture, with a similar trend at the shallowest soil depth (0–10 cm). The disparity between *M. ringens*' AGB and BGB can be partly attributed to its extensive adventitious roots deployed above the soil surface in standing water that were counted towards AGB. *C. vulpinoidea* reduced horizontal spread in all mixtures, basal circumference in FG 4, cover in FG 3 and vertical height and AGB in FG 3 and FG 4 compared to in monoculture. *C. vulpinoidea* also exhibited a substantial decline in BGB with –56% in FG 4 compared to monoculture, though this difference was not significant. *J. effusus*' AGB was lower in FG 4 than in monocultures, but this variation by richness level was not reflected by changes to its basal circumference, cover, stem length, or BGB. The difference in the reed's root expansion at 10–20 cm depth reflects a difference between the highest two richness levels.

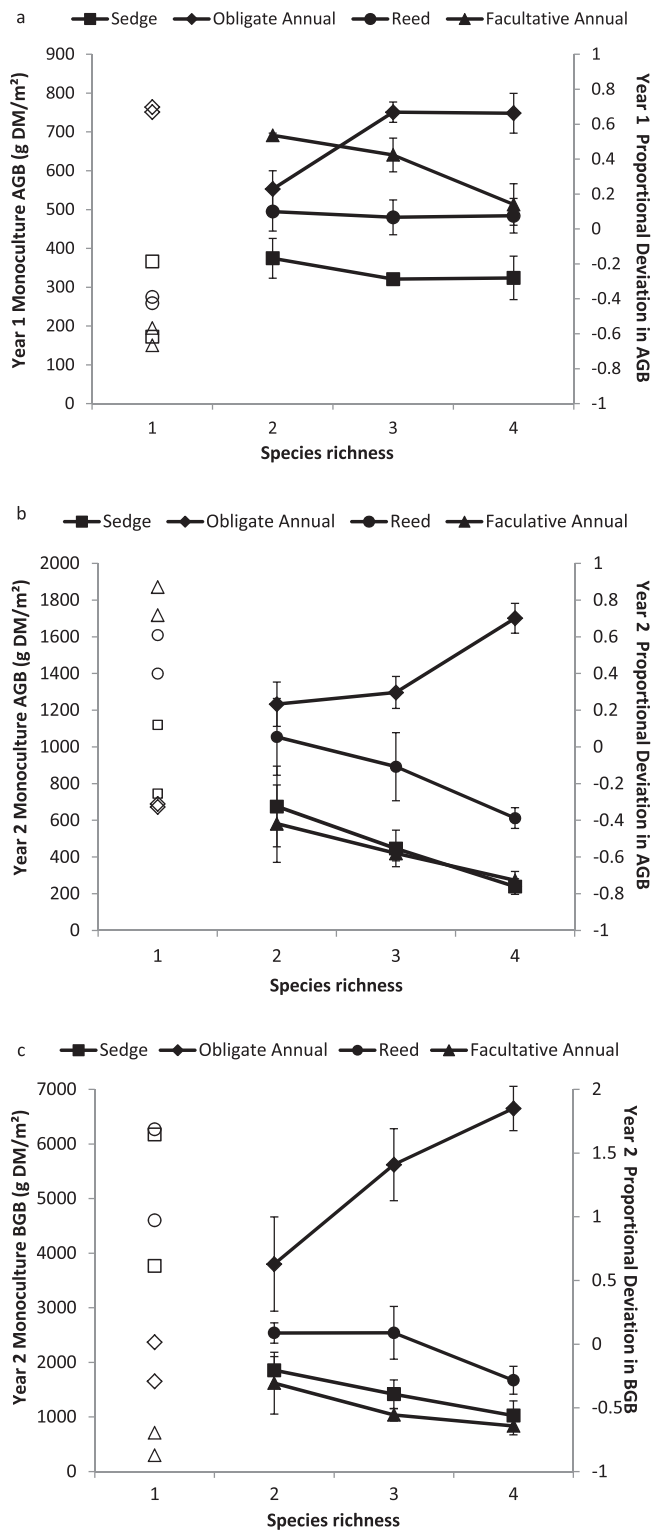


Figure 1: primary axis: mesocosm biomass of species monocultures for species richness = 1. Secondary axis: the mean proportional deviation, D_i , of species biomass in mixtures for species richness levels 2–4 expressed as a deviation from the expected biomass of that species on the basis of the original planting density of individuals. $D_i > 0$ where species produced more biomass in mixture than expected from monoculture and $D_i < 0$ where species produced less biomass in mixture than expected from monoculture. Open (primary axis) and closed (secondary axis) symbols represent *Carex vulpinoidea* (sedge), *Eleocharis obtusa* (obligate annual), *Juncus effusus* (reed) and *Mimulus ringens* (facultative annual) and are consistent between the two axes. Bars represent ± 1 standard error.

In contrast, *E. obtusa* increased its AGB and cover in FG 4 compared to FG 1. Similarly, *E. obtusa* increased its BGB in FG 3 and FG 4 compared to in monoculture, which was reflected at 0–10 cm and 10–20 cm depths.

Species' above- and belowground responses to community richness in the second year were highly correlated (Fig. 1b and c). The obligate annual substantially increased its relative contribution to community biomass production from 14% (AGB) and 16% (BGB) in monoculture to 41% (AGB) and 48% (BGB) in FG 4 mesocosms, with a moderately strong correlation between AGB and BGB proportional deviations ($r = 0.50$, $P = 0.02$). The sedge and facultative annual both reduced their aboveground and belowground relative contributions to community biomass production, with moderately strong ($r = 0.66$, $P = 0.001$) and strong ($r = 0.80$, $P < 0.001$) correlations, respectively. The reed's contribution to community biomass production was less variable across richness levels but the correlation in proportional deviations in AGB and BGB remained strong ($r = 0.79$, $P < 0.001$); thus, species richness had a weak negative effect on the BGB of the reed. As such BGB:AGB ratios varied little across richness levels for the reed [$F(3,30) = 0.820$, $P = 0.493$], sedge [$F(3,30) = 1.656$, $P = 0.198$] and facultative annual [$F(3,30) = 0.930$, $P = 0.438$], and we found no evidence of a shift in biomass apportioning for these species when considering total biomass (Fig. 2). The obligate annual was the exception to this pattern with a significant change in BGB:AGB [$F(3,30) = 3.538$, $P = 0.026$] (Fig. 2). *E. obtusa* shifted its apportionment of biomass belowground in the most diverse mixtures, where its BGB:AGB in FG 4 mesocosms (5.0) was almost twice that of its ratio in monoculture (3.1).

Community biomass

Estimated Yr1 AGB of mesocosms did not differ by richness level (Fig. 3; Table 1). In the second year, plants achieved greater size and maturity increasing mesocosm AGB by 487 g DM/m² on average. Mean Yr2 AGB decreased with richness levels, with 530 g DM/m² less in FG 4 mesocosms than in monocultures on average (Fig. 3; Table 1). Most mesocosm BGB, 94% of roots, was distributed in the top 10 cm of soil, with 3.5% and 2.5% at 10–20 and 20–30 cm depths, respectively. A decline in root distribution to the deepest depth range was found with increasing richness (Table 2); FG 4 mixtures were reduced in BGB at this depth compared to FG 2 mixtures and were trend-wise but not significantly reduced by a mean (median) of 77% (64%) compared to monocultures. No differences in overall mean Yr2 BGB (>3000 g DM/m²) (Fig. 3) or the apportionment of AGB and BGB [$F(3,30) = 1.476$, $P = 0.241$] were found across richness levels.

Morphological traits as predictors of community biomass production

Most morphological traits significantly contributed to species-level multiple regression prediction equations of Yr2 AGB (Table 3). Cover was the most versatile predictor of AGB.

Table 2: statistical results for tests of differences in belowground biomass by depth range for the sedge, obligate annual, reed, facultative annual and the community between richness levels (FGs 1–4)

Soil depth	Test	Statistic	df	P
<i>Carex vulpinoidea</i> (S)				
≤30 cm	F	1.01	3,30	0.400
0–10 cm	F_w	2.19	3,15	0.131
11–20 cm	F_w	1.80	3,14	0.192
21–30 cm	F	1.42	3,30	0.256
<i>Eleocharis obtusa</i> (OA)				
≤30 cm	F	9.13	3,30	<0.001**
0–10 cm	F	13.1	3,30	<0.001**
11–20 cm	F	3.62	3,30	0.024*
21–30 cm	F_w	0.066	3,13	0.977
<i>Juncus effusus</i> (R)				
≤30 cm	F	1.01	3,30	0.400
0–10 cm	F	0.764	3,30	0.523
10–20 cm	F	3.16	3,30	0.039*
20–30 cm	F	1.22	3,30	0.319
<i>Mimulus ringens</i> (FA)				
≤30 cm	F	3.18	3,30	0.038*
0–10 cm	F	3.26	3,30	0.035*
10–20 cm	F_w	0.827	3,12	0.503
20–30 cm	F	0.393	3,30	0.759
Mesocosms (C)				
≤30 cm	F_w	0.254	3,14	0.857
0–10 cm	F_w	0.220	3,14	0.881
10–20 cm	F_w	0.942	3,14	0.448
20–30 cm	F_w	4.14	3,14	0.027*

*P values significant at $\alpha = 0.05$. **P values significant at $\alpha = 0.01$.

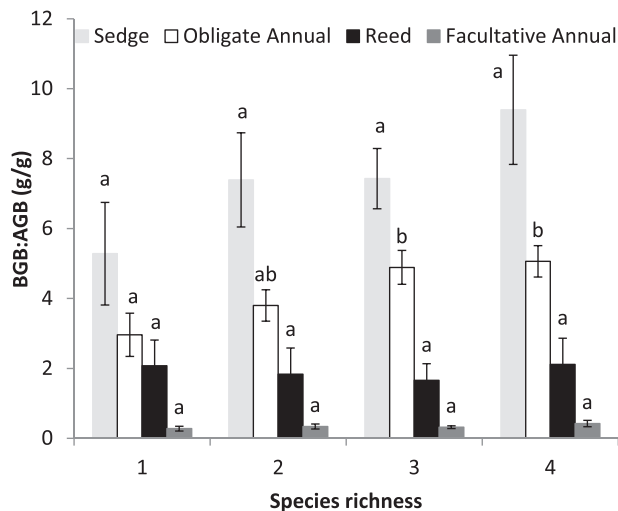


Figure 2: mean Yr2 BGB to AGB ratio for *Carex vulpinoidea* (sedge, light grey), *Eleocharis obtusa* (obligate annual, white), *Juncus effusus* (reed, black) and *Mimulus ringens* (facultative annual, dark grey) across species richness levels 1–4. Bars represent ± 1 standard error. Treatments not sharing a letter significantly differ at $P < 0.05$.

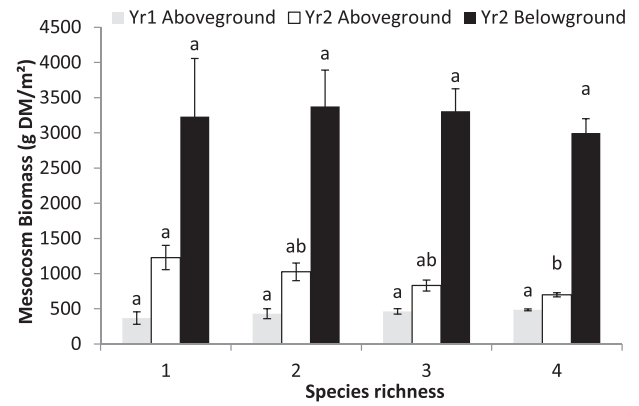


Figure 3: mean estimated Yr1 aboveground biomass (white), Yr2 aboveground biomass (black) and Yr2 belowground biomass (grey) by diversity level (FGs 1–4) for mesocosms. Bars represent ± 1 standard error. Treatments not sharing a letter significantly differ at $P < 0.05$.

Canopy and stem, height or length, were useful for all species except *E. obtusa*, who's variation in canopy height (46–50 cm) across richness levels was negligible. Species-specific predictors included canopy diameter and basal circumference for *C. vulpinoidea* and stem count for *M. ringens*. Due to the good model fit of the AGB regression equations, morphological traits were used to estimate Yr1 AGB of species and mesocosms.

Six morphological traits met the criteria for strong and significant correlations with species AGB in FG 4 mesocosms: stem count and cover for *M. ringens*; canopy diameter, cover and basal circumference for *C. vulpinoidea*; and basal circumference for *J. effusus*. Cover was used to represent the obligate annual in the community prediction equations because it was significantly related to AGB across all richness levels. We consider three of the six possible regression equations supportive, although two with greater uncertainty ($P \leq 0.10$), of the hypothesis that species individual traits can be used to predict community productivity (Table 4).

Partitioning richness effects

All mean richness effects for Yr1 AGB were positive, where grand means for NE (94.8 g DM/m²), CE (62.9 g DM/m²) and SE (31.9 g DM/m²) and their 95% confidence intervals across all mixtures fell entirely above zero (Fig. 4a). Despite the insignificant ANOVA results for mesocosm AGB across richness levels, all mixtures but one (FG 3) nontransgressively overyielded and had higher Yr1 AGB yields than the average monoculture. Selection effects significantly increased from FG 2 to FG 4 [$F(2,23) = 6.007$, $P = 0.008$], at which point they were of similar magnitude to CE, while no changes across mixture richness were found for CE [$F(2,23) = 0.111$, $P = 0.895$] or NE [$F(2,23) = 1.687$, $P = 0.207$] (Fig. 4a). Any fluctuations around the point estimates of Yr1 AGB for any of the species would not have changed the findings of a positive richness effect in the first

Table 3: species Yr2 aboveground biomass multiple regression equations constructed from morphological trait predictors for the sedge (*Carex vulpinoidea*), obligate annual (*Eleocharis obtusa*) (Willd.) Shult. (obligate annual), *Mimulus ringens* L. (facultative annual), *Juncus effusus* L. (interstitial reed) and *Carex vulpinoidea* Michx. (interstitial tussock), reed (*Juncus effusus*) and the facultative annual (*Mimulus ringens*)

Species	Regression equation	R^2_{adj}	df	F	P
<i>C. vulpinoidea</i>	$AGB^a = 0.078(CD) + 0.106(CH) + 0.085(BC) + 6.651(Cv) - 7.353$	0.849	4,29	47.46	<0.001**
<i>E. obtusa</i>	$AGB^b = 0.480(Cv^a) + 2.017$	0.603	1,32	51.14	<0.001**
<i>J. effusus</i>	$AGB^b = 0.012(SL) + 0.558(Cv) + 0.886$	0.571	2,31	23.00	<0.001**
<i>M. ringens</i>	$AGB^b = 0.007(SH) + 1.996(Cv) + 0.003(SC) + 1.167$	0.883	3,30	83.87	<0.001**

Abbreviations: AGB = aboveground biomass (g); CD = canopy diameter (cm); CH = canopy height (cm); BC = basal circumference of clumped growth (cm); Cv = cover estimate of canopy spread (cm²); SL = mean stem length (cm); SH = mean stem height (cm); SC = stem count.

^asquare-root transformed.

^bLog₁₀ transformed. ** P values significant at $\alpha = 0.01$.

Table 4: best-fitting aboveground biomass multiple regression equations for the most species-rich community (FG 4) constructed from species morphological trait predictors in the second year

Y	=	<i>Carex vulpinoidea</i>	+	<i>Eleocharis obtusa</i>	+	<i>Juncus effusus</i>	+	<i>Mimulus ringens</i>	+	Intercept	R^2_{adj}	df	F	P
AGB ^a		0.002 (CD)		0.192 (Cv ^b)		0.005 (BC)		0.354 (Cv)		2.229	0.815	4,3	8.710	0.053
AGB ^a		0.009 (BC)		0.191 (Cv ^b)		0.001 (BC)		0.004 (SC)		2.205	0.725	4,3	5.611	0.094
AGB ^a		0.002 (CD)		0.203 (Cv ^b)		0.005 (BC)		0.002 (SC)		2.214	0.864	4,3	12.128	0.034*

Abbreviations: AGB = aboveground biomass (g/m²); BC = basal circumference of clumped growth (cm); CD = canopy diameter (cm); Cv = cover estimate of canopy spread (cm²); SC = stem count.

^aLog₁₀ transformed. ^bsquare-root transformed. * P values significant at $\alpha = 0.05$.

year nor appreciably changed the strength of the effect. The obligate annual had a large influence during the first year (Fig. 1a). Indeed, the three lowest yielding mesocosms at both FG 2 and FG 3 levels in the first growing season did not contain the obligate annual.

In the second growing season, all mean AGB richness effects for all richness levels were negative; grand means of NE (−394 g DM/m²), CE (−287 g DM/m²) and SE (−107 g DM/m²) and their 95% confidence intervals all fell entirely below zero (Fig. 4b). A negative NE reflects lower average production in mixtures (−394 g DM/m²) compared to the average monoculture. Negative interactions strengthened across mixture richness for NE [$F(2,23) = 4.241$, $P = 0.027$] and SE [$F(2,23) = 3.775$, $P = 0.038$], but not CE [$\chi^2 = 4.061$, $P = 0.131$] (Fig. 4b). We examined the effect of *E. obtusa* on community productivity: Three mixtures, all without the obligate annual, displayed positive richness effects, while the other three mixtures with the obligate annual displayed all negative NE, CE and SE.

The overall richness effects for BGB were not significant: 95% confidence intervals for the grand means of NE (−3.23 g DM/m²), CE (176 g DM/m²) and SE (−180 g DM/m²) all included zero (Fig. 3c). Neither were there significant relationships of NE [$F(2,23) = 0.562$; $P = 0.578$], CE [$F(2,23) = 0.307$, $P = 0.739$] or SE [$F(2,23) = 1.663$, $P = 0.211$] for BGB across mixture richness levels (Fig. 4c). Although the mean BGB selection effect (−527 g DM/m²) for FG 4 was significant (mean \pm 1.96 standard error < 0), its contribution to the NE was negated by the more positive CEs. The presence of the obligate annual reduced belowground total community

productivity. The three mesocosms in both FG 2 and FG 3 that did not contain the obligate annual (*E. obtusa*) all performed better on average: three non-*E. obtusa* mesocosms in FG 2 were among the four with highest BGB, and the three non-*E. obtusa* mesocosms in FG 3 all attained the highest BGB.

DISCUSSION

Diversity–productivity relationships

A large majority of plant diversity–productivity studies in experimental systems have found greater biomass production in more diverse (e.g. species and functional group richness) plant communities (Cardinale *et al.*, 2007). In our case, the slightly positive effects of plant functional richness on community biomass production in the first year were transient. We found that the positive effects of species richness in the first growing season, when mixtures produced 1.25 times greater AGB than monocultures, became negative in the second season, when monocultures produced 1.44 times more biomass than mixtures. The meta-analysis by Cardinale *et al.* (2007) revealed that the reported overall positive richness effect on productivity may mask more idiosyncratic (i.e. neutral to negative) results of certain underyielding mixtures at lower richness levels. The negative diversity effects found by Polley *et al.* (2003) in a study of a mixture of three annuals planted across varying densities and evenness corroborates this notion. These findings together with ours suggest that the diversity–productivity relationship is partly shaped by the number of species richness levels or the number of different communities studied.

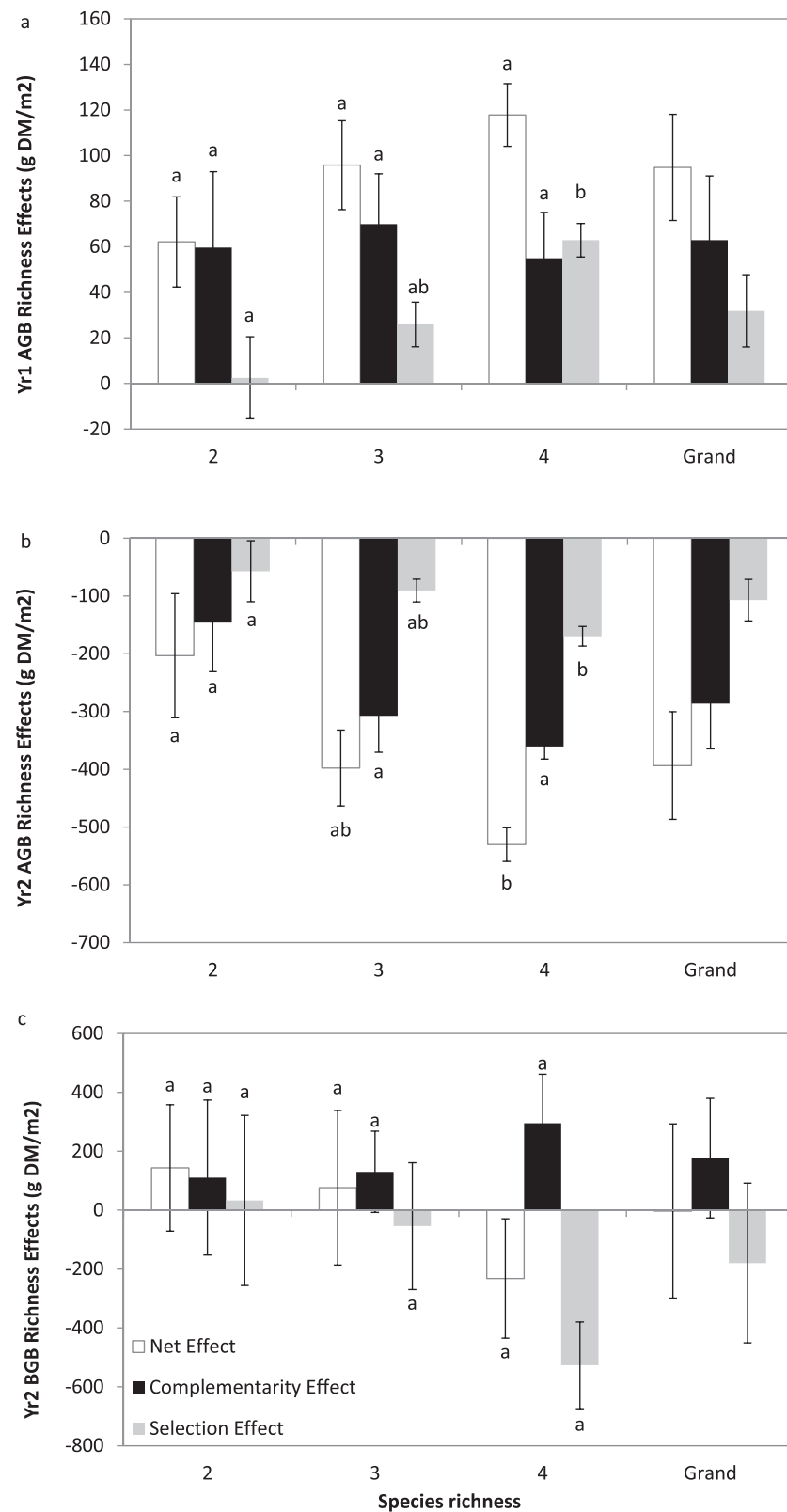


Figure 4: mean community net effect (white), complementarity effect (black) and selection effect (grey) at each mixture diversity level (FGs 2–4) and across all mixtures (Grand) for Yr1 aboveground biomass (a), Yr2 aboveground biomass (b) and Yr2 belowground biomass (c). Bars for diversity levels 2–4 represent ± 1 standard error; bars for grand mean represent 95% confidence interval. Treatments not sharing a letter significantly differ at $P < 0.05$.

In spite of the inhibition present in our experimental mixtures, our study conforms to other established conceptual patterns from large-scale diversity–productivity experiments. One such experiment, a multi-site experiment in grasslands conducted by Spehn *et al.* (2005), found that biomass production and diversity effects were usually lowest during the first year of the experiment and that diversity effects on AGB were stronger than BGB. Consistently, we found that the effects of richness on AGB strengthened in magnitude in the second growing season indicating that the size or maturity of plants more than the type of species interaction has a strong mediating influence on the diversity outcome. Additionally, overall richness effects were stronger aboveground than belowground in our study. Complementarity effects remained consistent across mixture richness levels and were either relatively equal to (Yr1 AGB and Yr2 BGB) or greater than selection effects (Yr2 AGB). The trends in strengthening selection effects, which occurred across richness levels in both years, relate to the performance of the obligate annual; however, *E. obtusa* had a strong but not singular influence on mixture performance. Large variation also existed for the other species' proportional yields in mixtures.

Species traits and interactions

Similar to Thein *et al.* (2008), we found that species exhibited morphological plasticity in aboveground traits (e.g. stem and canopy height) between monocultures and mixtures and that the degree of consistency with changes in biomass production was species-dependent. Where biomass production was variable, species did respond with changes to morphology. Trait variability in the obligate annual (i.e. stem density) and the facultative annual (i.e. height) corresponded to changes in AGB in the first year. In the second year, many species' fitness levels were impaired and morphological plasticity corresponded with reductions in AGB for the facultative annual and sedge. The reed, by contrast, maintained its basal circumference, cover and stem length while reducing overall AGB, possibly indicative of a competitive response in tolerance of competition and concomitant nutrient or resource deficiencies (Keddy *et al.* 1998).

Community richness had a weak effect on the BGB of mesocosms, whereby the most diverse mixtures distributed fewer roots at depths >20 cm than in monocultures. Plasticity in root distribution at this depth was not found at a species level, though all species exhibited a trend-wise reduction, but was an emergent attribute at the mesocosm level. In investigating whether species differences or plasticity in rooting depth in grassland plants could explain plant complementarity in belowground productivity, von Felton and Schmid (2008) found that having a sufficient volume of soil for root growth was a more important determinant of plant complementarity than soil depth, possibly due to the energetic constraints of resource extraction from deeper zones. In another study of natural root distribution and abundance in grasslands, Frank *et al.* (2010) concluded that root segregation played a minor role in species coexistence and that

the majority of plant species under study were randomly distributed by depth. The lack of oxygen in the mesocosms—our wetland soils remained consistently anaerobic in the second year (authors' unpublished data)—might have contributed to less vertical root expansion overall.

In spite of decreasing rooting depth, no changes in BGB were observed at a mesocosm level. These results contrast with other studies in wetlands that have reported positive correlations between BGB and species richness (Bouchard *et al.* 2007; Callaway *et al.* 2003; Schultz *et al.* 2012), and specifically positive correlations between increasing BGB and depth of root deployment (Bouchard *et al.* 2007). Here, we can look mechanistically at species contributions to BGB. Community richness negatively affected the BGB of the facultative annual, weakly negatively affected the sedge and reed and strongly positively affected the obligate annual. *E. obtusa* greatly expanded its BGB relative to AGB in mixtures (Fig. 3) and its proportional deviations belowground were almost twice that aboveground at the highest richness level (Fig. 1b and c). Species contributing most to BGB in the most diverse mixtures (~96% BGB), the sedge, reed and obligate annual, all exhibited greater complementarity (or weaker inhibition) belowground than aboveground.

Factors mediating biomass partitioning above and belowground are not well understood but may be species-specific and depend on stress and medium of competition (Bessler *et al.* 2009; Burns and Strauss 2011; Kiaer *et al.* 2013). The reduction in AGB suggests that light or nutrient resources were constrained in FG 4 mesocosms. Comparisons to other natural and created freshwater wetlands indicate that the experimental mesocosms simulated soil conditions typical of created wetlands and can be classified as a low nutrient system on the basis of total carbon and nitrogen content (Bailey *et al.* 2007; Ballantine and Schneider 2009; Dee and Ahn 2012; Stauffer and Brooks 1997). While topsoil removal can be a successful approach to remediate effects of previous landuse practices, such as fertilization or native plant seed bank depletion (Bakker 2013; Klimkowska *et al.* 2010), topsoil application in created and restored wetlands has been shown to have beneficial effects on the plant community (Stauffer and Brooks 1997). Thus, limitation in soil nitrogen or other nutrients might have contributed to species above and belowground performances in this study. Limited nutrients can promote symmetric root competition, whereby root foraging ability is linearly related to the volume of soil exploited, and may partly explain the lack of richness effects on community BGB (Frank *et al.* 2010; von Wettberg and Weiner 2003). By the same token, the obligate annual engaged in asymmetric competition by increasing its BGB:AGB ratio across the species richness gradient. A game-theory model of annual plant behavior postulates that in the presence of competitors an annual will produce greater roots than optimal for reproductive fitness in a 'tragedy of the commons'-type scenario (Gersani *et al.* 2001; O'Brien *et al.* 2005).

Morphological traits predict community biomass production

Estimating peak AGB, BGB or other metrics of primary productivity using species morphological traits have a long tradition in plant ecology (Carpenter 1980; Dickerman *et al.* 1986; Mathews and Westlake 1969; Whigham and Simpson 1978; Wetzel and Pickard 1996) and can be beneficial to the ecosystem by reducing disturbance caused by destructive harvesting, particularly in the case of repeat evaluation. Biomass accumulation is a good indicator of wetland ecosystem development as it relates to plant-driven carbon processing, and can be used as success criteria in evaluating the functional maturation of compensatory wetland creation and restoration. Our biomass results comport with reported biomass values in the literature for herbaceous, emergent vegetation in freshwater nontidal marshes of similar hydrology of the current mesocosm experiment (Cole *et al.* 2001; Kao-Kniffin *et al.* 2010; Stefanik and Mitsch 2012; Wetzel and Howe 1999) and can be presumed to represent natural communities. We found tight responses between morphological traits and AGB across a gradient of interspecific interactions holding abiotic factors constant. Traits such as cover, stem height or basal circumference contributed significantly to the equations and are easy and fast measurements to make. Counts of stem number are potentially strong predictors of AGB but can be laborious or impractical in many species for timely evaluations of plant performance.

We specifically investigated the ability to predict community biomass production using species traits. Three of the six regression equations were significant and with good model fit, demonstrating that morphological traits can be good predictors of both species and community AGB. Since more morphological traits were significant predictors of species-level AGB as generalized across richness levels, we infer that our morphological traits might be better predictors of community AGB with a greater range of species richness or abiotic variability. Our prediction equations constructed from varying morphological measures are specific to the plant community in this study but demonstrate that targeted species-dependent trait measurements may increase the accuracy of community productivity estimates. We also investigated root:shoot ratios and the explanatory power of AGB on BGB. Three of the species conserved their BGB:AGB ratios across the species richness gradient and all species had moderately strong to strong positive correlations in proportional root and shoot biomass deviations. That most of the species did not demonstrate plastic responses in biomass partitioning can be useful to managers who want to use aboveground performance or competition as a proxy for belowground interactions (Cahill 2002).

Competitive dominance

Species dominance may exert a large influence on community condition through the suppression of other species, regulation

of resource levels and control of nutrient cycling (Frieswyk *et al.* 2007). Multiple lines of evidence suggested that the dominance by the obligate annual partly contributed to the pervasive community interference in the second growing season. For instance, the absence of *E. obtusa* was associated with the highest BGB yields. In the most diverse mixtures, the obligate annual achieved the highest abundance and cover of any species. In the first growing season, *E. obtusa* accounted for an average of 68% of total species cover in the most diverse mixtures; in the second growing season, this number dropped to 46%, on average, compared to 18%, 12% and 7% on average for the reed, sedge and facultative annual, respectively. More evenness in cover, but not abundance, was found at FGs 2 and 3. The obligate annual also out-produced the other species in the most diverse mixtures in the second year while having below-average yields in monocultures, which suggests a trade-off in functional performance and competitive ability. We conclude that the community inhibition was not solely an artifact of having a lower yielding species in mixtures, but was primarily a result of asymmetric competition driven by *E. obtusa*.

Predictions of community productivity on the basis of species' monoculture yields are difficult in communities substantially dominated by few species, and more difficult if dominated by underyielding species, effects inconsistent with traditional sampling models (Hector *et al.* 2002a). The monoculture productivity in our study poorly corresponded to mixture productivity in the second year; instead, the functional traits related to growth rate were good indicators of a dominant competitor and of community dominance. Dominant competitors have been shown to mitigate the positive interactions leading to higher species productivity (Engelhardt and Ritchie 2001; Hector *et al.* 2002b). Doherty *et al.* (2011) showed that species dominance across plots from a re-visited saltmarsh diversity study (Callaway *et al.* 2003) can eventually reverse early positive richness effects and lead to reduced performance in species-rich mixtures. In this study, dominance by a ruderal species suppressed community establishment from the beginning. Other wetland diversity studies using species of equivalent functional groupings to ours have nonetheless found positive diversity-productivity relationships in the second and third growing seasons of their experiments (Bouchard *et al.* 2007; Schultz *et al.* 2012). In particular, Schultz *et al.* (2012) found transgressive overyielding of diverse mixtures with a relatively small selection effect at the highest species richness level, which does not suggest species dominance and suppression of species performances. Our results may diverge from theirs because the treatment effect of richness in our study tested for differences between interspecific interactions in mixtures and intraspecific interactions in monocultures, and not for differences from interspecific interactions only. Additionally, obligate annuals were introduced to mixtures in the second growing season in Schultz *et al.*'s study to allow other functional groups to establish. Diversity effects have been found to be stronger with more

numerous species (Schmid *et al.* 2009); planting multiple obligate annuals with equivalent functional abilities may have a positive effect on overall yields of young communities.

Implications for wetland creation

The abilities to spread and generate more than one generation in a growing season are key traits that can be constraints on early planted wetland communities. In a disturbed community below ecological carrying capacity, early successional species can temporarily out-perform co-occurring later successional species through rapid growth (Pacala and Rees 1998). Successional niches describe a colonization–competition trade-off, or strategies to optimize seed production and establishment at the expense of growth and longevity. As an extension, here we show that strong interference and lower productivity may be expected in newly planted ecosystems where ruderal strategies are initially favored, a potentially important component shaping the relationships between diversity and community productivity. We also show that not all combinations of functionally diverse species promote community biomass production. Without replicating species within functional group richness levels, we are unable to conclude that these results are robust to community compositional changes; however, we described mechanisms responsible for negative diversity–productivity relationships that may operate in early wetland planting communities. Matthews and Endress (2010) found that site characteristics other than age in restored wetlands were better determinants of plant community succession from predominantly annuals to more clonal, perennial species. In particular, the authors found that under nutrient limiting conditions, annual or ruderal species maintained dominance in the restored communities into the fourth year.

The results of this study inform restoration practices intended to promote productivity in planted macrophyte communities in created wetlands. Whether seeded, planted, or recruited, *E. obtusa* and its ilk are likely to proliferate naturally in the first few years until later successional species fully establish. Attempts to completely bypass this development stage by introducing perennials in the first growing season may be unsuccessful by themselves; rather, because this study demonstrated that species competed more strongly above-ground, restoration practices that alleviate uncontrollable shoot interference may be beneficial to community productivity. Less systematic planting designs such as clustering the same or similar species will vary the density and structure of plant canopies which could reduce widespread competition from monopolizing species (Twedt 2006). Alternatively, engineering design elements fostering spatial or temporal environmental variability (e.g. microtopography) in newly created wetlands helps diversify the responses of wetland macrophyte species to their environment (Moser *et al.* 2007) and could allow for greater complementarity in biomass production in light of competitive interference.

CONCLUSIONS

We conducted a 2-year diversity–productivity experiment using freshwater wetland mesocosms to investigate biomass production as affected by macrophyte functional group richness that can be introduced as a design element in created wetlands. The positive effect of species richness on AGB was shown to be transient, and interspecific interference drove negative community dynamics in the second season. A dominant competitor, in this case a ruderal, annual species, disproportionately influenced community performance and inhibited community biomass in the second year. Good agreement was found between plant morphological trait plasticity and biomass production, as well as species above- and belowground performances across a species richness gradient. Our study highlights the need for additional research on the functional performance of other potentially dominant species, such as matrix species not studied here, in the context of early planting designs that will help improve our understanding of plant community development and its impacts on ecosystem development in newly created wetlands.

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Conflict of interest statement. None declared.

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